

# $\delta^{15}\text{N}$ Patterns of Douglas-Fir and Red Alder Riparian Forests in the Oregon Coast Range

Emily E. Scott, Steven S. Perakis, and David E. Hibbs

**Abstract:** We used naturally occurring stable isotopes of N to compare N dynamics in near-stream and upslope environments along riparian catenas in N-fixing red alder (*Alnus rubra*) and Douglas-fir (*Pseudotsuga menziesii*) forests in the Coast Range of western Oregon. Based on the existing literature, we expected soil  $\delta^{15}\text{N}$  to be enriched closer to streams owing to inputs of isotopically heavy, marine-derived N by spawning salmon, higher rates of denitrification near the stream, or both. However, it has been unclear what effect red alder might have on soil  $\delta^{15}\text{N}$  patterns near streams. We found a consistent  $-1\text{‰}$   $\delta^{15}\text{N}$  signature in red alder foliage, and  $\delta^{15}\text{N}$  of total N in soils under red alder averaged  $2.2\text{‰}$  along sampling transects extending 20 m upslope from the stream. Surprisingly,  $\delta^{15}\text{N}$  of total N in soil under Douglas-fir was progressively depleted nearer to streams, opposite from the pattern expected from N losses by denitrification or N inputs from anadromous salmon. Instead,  $\delta^{15}\text{N}$  of total N in soil under Douglas-fir converged toward soil  $\delta^{15}\text{N}$  values typical of red alder sites. We consider that the historic presence of red alder may have contributed a legacy of lower soil  $\delta^{15}\text{N}$  nearer to streams on sites that are currently dominated by young Douglas-fir forest. *FOR. SCI.* 54(2):140–147.

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**R**IPARIAN ZONES provide a complex environment for studying N biogeochemistry owing to interactions between the terrestrial and aquatic systems. These interactions can occur via exchanges in organic materials, such as terrestrial inputs of leaf litter to streams (Gregory et al. 1991) or, in some regions, the supply of decaying carcasses from spawning salmon to streamside environments (Helfield and Naiman 2002). These systems can also interact through denitrification in saturated soils along a stream where N in terrestrial runoff is converted into gaseous forms, thereby decreasing the amount of N entering the aquatic system (Hedin et al. 1998).

In riparian areas of the Coast Range of western Oregon, an additional feature influencing N cycling is the presence of red alder (*Alnus rubra* Bong) in riparian forests. Pure stands of red alder can sustain high rates of N fixation, up to  $200 \text{ kg of N ha}^{-1} \text{ yr}^{-1}$  (Binkley et al. 1994), which increases soil N (Luken and Fonda 1983), accelerates N cycling over 50–100 years of stand growth (Turner et al. 1976, Binkley et al. 1992, 1994), and promotes N leaching from forests (Compton et al. 2003). Red alder is an early successional species that codominates riparian forests to varying extents with Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], another pioneer species (Pabst and Spies 1998, Nierenberg and Hibbs 2000). Red alder tends to decrease in abundance with distance from a stream (Nierenberg and Hibbs 2000).

Naturally occurring stable isotopes of nitrogen ( $\delta^{15}\text{N}$ ) may provide a useful tool to better understand N dynamics

in riparian environments. Previous studies in upland systems have used  $\delta^{15}\text{N}$  to infer N cycling rates from plant and soil  $\delta^{15}\text{N}$  (Garten 1993, Garten and Van Miegroet 1994, Koopmans et al. 1997, Emmett et al. 1998, Pardo et al. 2002, Koba et al. 2003), analyze plant N uptake via mycorrhizal associations (Hobbie et al. 1999a, 1999b, 2000, Hobbie and Colpaert 2003), determine the depth and form of soil N uptake by plants (McKane et al. 2002), and estimate ecosystem-level N balances (Johannisson and Högberg 1994). In riparian areas,  $\delta^{15}\text{N}$  has been used to trace marine-derived N from anadromous fish to near-stream soils and plants (Ben-David et al. 1998, Helfield and Naiman 2001, 2002, Bilby et al. 2003, Reimchen et al. 2003) and evaluate denitrification in saturated soils (Hedin et al. 1998).

In general, vegetation  $\delta^{15}\text{N}$  reflects that of its N source or sources (Shearer and Kohl 1986), providing a means of tracing N in an ecosystem. For example, plants that fix atmospheric  $\text{N}_2$  have demonstrated a fairly narrow range of  $\delta^{15}\text{N}$ , between  $-2.0\text{‰}$  and  $2.0\text{‰}$ , which reflects the atmospheric  $\delta^{15}\text{N}$  of  $0\text{‰}$  (Shearer and Kohl 1986). However, the relationship between plant and soil  $\delta^{15}\text{N}$  is not necessarily as straightforward (Robinson 2001). Fractionation during N uptake and assimilation can decouple the plant-soil  $\delta^{15}\text{N}$  relationship (Evans 2001). Also, small-scale variations in  $\delta^{15}\text{N}$ , both horizontally and with depth (Nadelhoffer and Fry 1988), may also contribute to plant  $\delta^{15}\text{N}$  heterogeneity, depending on which N pool a particular plant was accessing. These small-scale variations in soil  $\delta^{15}\text{N}$  can result from soil

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N transformations, such as nitrification, in which fractionation produces distinct  $\delta^{15}\text{N}$  for different soil N pools (Högberg 1997). The dynamic nature of these pools can result in changes of pool  $\delta^{15}\text{N}$  over short time scales as N is removed from the system via plant uptake or leached from the soil environment. Conversely, total soil N is larger and less dynamic than plant-available N pools and requires greater time to acquire, or lose, its isotopic signature.

Despite potentially high  $\delta^{15}\text{N}$  variability, plant and soil  $\delta^{15}\text{N}$  can still provide useful insights into N cycling and controls on  $\delta^{15}\text{N}$  patterns. Worldwide, foliar  $\delta^{15}\text{N}$  signatures are consistently depleted relative to surface soil  $\delta^{15}\text{N}$  pools (Martinelli et al. 1999, Amundson et al. 2003). Garten and Van Miegroet (1994) used this feature to create a metric, which they termed an “enrichment factor” ( $\epsilon_{\text{p-s}}$ ), that related the difference between plant and soil  $\delta^{15}\text{N}$  to the N fertility of a particular site. Narrow  $\delta^{15}\text{N}$  discrepancies between plants and soils (i.e.,  $\epsilon_{\text{p-s}}$  approaching 0) were correlated with indices of high N availability and were thought to result from plant uptake of soil ammonium that was enriched during incomplete nitrification (Garten and Van Miegroet 1994). Other studies have found similar relationships between enrichment factors and the N fertility of a site (Koopmans et al. 1997, Emmett et al. 1998, Pardo et al. 2002, Koba et al. 2003), although lower net fractionation of plant-available N by mycorrhizae at high N availability may also explain this pattern (Hobbie et al. 1999b, Hobbie and Colpaert 2003).

In this study, we use the  $\delta^{15}\text{N}$  of canopy tree foliage and soil to compare N dynamics in near-stream versus upslope environments in the Coast Range of western Oregon. Based on our understanding of riparian areas in the Pacific Northwest, we expect bulk soil  $\delta^{15}\text{N}$  near streams to be more enriched compared with soils upslope for one or both of the following reasons: N inputs from spawning salmon (*Oncorhynchus* spp.) in the Pacific Northwest contribute isotopically heavy N inputs ( $>10\%$ ) to near-stream forests (Ben-David et al. 1998, Helfield and Naiman 2002, Reimchen et al. 2003) or the loss of depleted N gasses from denitrification in saturated soils (Hedin et al. 1998) could result in enriched soil  $\delta^{15}\text{N}$  near streams. However, it is unclear whether red alder also influences the  $\delta^{15}\text{N}$  of foliage and soils in these forests. Isotopic studies of alder species have demonstrated a narrow range of  $\delta^{15}\text{N}$  for foliage (Binkley et al. 1985, Hurd et al. 2001) that, when combined with the ability of red alder to contribute large amounts of fixed N to soils, may have the potential to drive patterns of soil  $\delta^{15}\text{N}$ . The decreased dominance of red alder away from streams in favor of conifers (Nierenberg and Hibbs 2000) allows for a potential gradient of red alder influence on soil N with greater distance from a stream. Therefore, to determine whether our predictions of riparian  $\delta^{15}\text{N}$  patterns hold true with and without the presence of red alder, we selected five sites in riparian forests where red alder dominated the canopy and five where Douglas-fir was the dominant species. We sampled foliage, fresh leaf litter, forest floor material, and bulk soil at each site and compared the  $\delta^{15}\text{N}$  and %N of these fractions between the two canopy types. Our interest in whether fixed-N from red alder may affect riparian  $\delta^{15}\text{N}$  led us to focus on total rather than inorganic N

pools, as inorganic N pools are highly transient and subject to strong temporal variations in isotopic fractionation that may not accurately reflect longer-term N inputs and cycling. Total soil N concentrations also correlated strongly with plant tissue and soil inorganic N concentrations in Coast Range forests, suggesting broad cohesion across N cycling metrics in these forests (Perakis et al. 2006). However,  $\delta^{15}\text{N}$  of plants and soils in these forests remain largely unexplored.

## Methods

### Study Area

The study occurred in the central Coast Range of western Oregon in the Upper Alsea, Lake Creek, and Lower Siuslaw watersheds. The riparian soils range from moderately deep sandy loams to clay loams with dark surface horizons high in organic matter (Corliss 1973, Patching 1987). The maritime climate is moderate with warm, dry summers and cool wet winters. Rain is the dominant form of precipitation and falls mostly from October to March with annual rainfall between 150 and 300 cm. The study area falls in the western hemlock coniferous vegetation zone with major forest tree species of Douglas-fir, western hemlock [*Tsuga heterophylla* (Raf.) Sarg.], and western redcedar (*Thuja plicata* Don ex D. Don) (Franklin and Dyrness 1988). Red alder and bigleaf maple (*Acer macrophyllum* Pursh) are common deciduous species.

Our 10 riparian forests were located on Bureau of Land Management lands within 50 km of the Pacific Ocean with a north/south range of 80 km. The sites were adjacent to second- to fourth-order streams with constrained reaches. Sites were selected qualitatively on the basis of the relative dominance of red alder in the canopy; sites either contained a pure stand of red alder or a stand dominated by Douglas-fir with no/few red alder present. We assumed that the influence of any red alder on overall site N patterns on Douglas-fir-dominated sites would be minimal based on the results of Rhoades and Binkley (1992) who found that the influence of red alder on N availability in forests was restricted to a downslope direction. The points at which we sampled Douglas-fir trees and soils on the plots were either in-line with, or upslope from, the red alder present along the stream. We additionally minimized potential delivery of red alder N from upslope areas by careful selection of Douglas-fir riparian sites without upslope red alder (Rhoades and Binkley 1992). Some stands had a small component of bigleaf maple, western hemlock, and/or western redcedar. The median dbh of red alder across our sites was 38 cm (range 27–44 cm); for Douglas-fir, the median dbh was 53 cm (range 46–107 cm).

Tree age ranged from 30 to 60 years for red alder and from 40 to 70 years, with one stand being more than 100 years of age, for Douglas-fir, placing the establishment of our stands at the time of midcentury logging. Postharvest tree planting was not a common practice at the time of stand establishment, suggesting that our stands were naturally regenerated. The irregular tree spacing supports this conclusion. Subsequent fires or management have not occurred in the stands. In the Oregon Coast Range, Douglas-fir does

not usually follow red alder in a successional sequence (Nierenberg and Hibbs 2000), but they may replace each other at a specific site after disturbances such as flooding, logging, or fire. Additionally, this region has a long history of salmon in all streams that are not above barriers. Only two of our sites, one red alder and one Douglas-fir, were located upstream of physical barriers to anadromy.

### Sample Collection

We established one plot at each of the 10 sites. Each rectangular plot was 50 m along the direction of the stream and approximately 20 m upslope from the edge of the active stream channel, depending on where the nearest tree to this upslope distance was located. We collected foliage samples from five canopy-dominant trees in each plot in summer 2002. Three of these trees were sampled along a transect 10 m upslope and parallel to the stream, at 0-, 25-, and 50-m positions. In the middle of each plot, two additional trees were sampled, one from near the stream edge and one 20 m upslope. To ensure similar light conditions, all foliage was collected from middle-to-upper canopy positions of stream-side branches using a shotgun. A composite sample of approximately 50–70 first year needles from Douglas-fir and 5 fully expanded leaves from red alder was collected from each tree, for a total of 5 foliage samples per site.

We collected bulk soil to measure the long-term  $\delta^{15}\text{N}$  signature of our soils (Högberg 1997). Also, bulk soil %N tracks well with plant-available soil N pools in Coast Range soils (Perakis et al. 2006). Soil samples were collected within 1–2 m of the base of sample trees. We collected Oi horizon material (which we refer to as “forest floor”) from an area of approximately 0.25 m<sup>2</sup> beneath each tree. Mineral soil was sampled to 10 cm depth with a 5-cm diameter corer. We collected fresh litterfall over a 1-week period in autumn 2002 using two suspended mesh traps (0.27 m<sup>2</sup> each) per plot.

### Chemical Analysis

Foliage, forest floor, and litterfall were dried separately at 50°C for 48 hours and ground to a fine powder. Soils were sieved (2 mm), dried at 60°C for 72 hours, and ground. Samples were analyzed by a PDZ Europa Scientific 20/20 mass spectrometer (Europa Scientific, Ltd., Crewe, UK) at the Berkeley Center for Stable Isotope Biogeochemistry, University of California at Berkeley, for  $\delta^{15}\text{N}$ , %N, and %C. Isotope values are expressed in delta notation ( $\delta$ ) referenced against atmospheric N<sub>2</sub> as the standard (i.e., atmospheric  $\delta^{15}\text{N} = 0\text{‰}$ ) (Peterson and Fry 1987). The precision of isotope analysis for replicate samples was within 0.17‰ for  $\delta^{15}\text{N}$ . An enrichment factor (the  $\delta^{15}\text{N}$  difference between plant foliage and soil:  $\epsilon_{\text{p-s}} = \delta^{15}\text{N}_{\text{plant}} - \delta^{15}\text{N}_{\text{soil}}$ ) was calculated to standardize differences between soil and foliage  $\delta^{15}\text{N}$  across sites as described by Garten (1993) and Garten and Van Miegroet (1994).

### Data Analysis

Comparison of average values between red alder versus Douglas-fir sites was done by *t*-test ( $n = 5$  for each vege-

tation type for all comparisons). Within each overstory type, data were analyzed using linear regression to compare trends among  $\delta^{15}\text{N}$ , %N, %C,  $\epsilon_{\text{p-s}}$ , and distance from the stream after accounting for spatial autocorrelations. To do this, we first determined the regression coefficients for a response variable on an independent variable for each of the five sites. Then, to represent overall site trends, we generated a weighted average of those regression coefficients that accounted for varied trend strengths at the five sites. All models had two main effects, with “site” as one of those main effects in each comparison. No interaction term between main effects was tested because we were not interested in patterns on individual sites, only overall site trends. Significance levels were set at  $\leq 0.05$  before the analysis. All statistical procedures were conducted using statistical software from the SAS Institute, Inc. (1999).

### Results

At Douglas-fir sites, soil  $\delta^{15}\text{N}$ , foliar %N, foliar  $\delta^{15}\text{N}$ , and enrichment factors were related significantly to distance from the stream (Table 1). Soil  $\delta^{15}\text{N}$  was related positively to distance from the stream (Figure 1a) and was progressively depleted at higher soil %N (Table 1). Soil  $\delta^{15}\text{N}$  and soil %C were unrelated (Table 1).  $\epsilon_{\text{p-s}}$  for Douglas-fir sites narrowed significantly toward  $-3.5\text{‰}$  closer to streams (Figure 1b; Table 1). N concentration and  $\delta^{15}\text{N}$  of Douglas-fir foliage were weakly but significantly greater near the stream (Figure 2). Foliar  $\delta^{15}\text{N}$  was not related significantly to foliar %N, soil  $\delta^{15}\text{N}$ , or soil %N (Table 1). There was no significant association of distance away from the stream with soil %N or soil %C (Table 1; Figure 1c). In sites dominated by red alder, we did not detect any significant relationships between distance from the stream and foliar %N or  $\delta^{15}\text{N}$ , soil %N, %C or  $\delta^{15}\text{N}$ , or enrichment factors (Table 1; Figures 1 and 2).

Red alder foliar %N ( $2.5 \pm 0.05\%$  [mean and SE],  $n = 5$  sites) was significantly greater than %N for Douglas-fir ( $1.2 \pm 0.03\%$ ) when considered across all sites ( $P < 0.001$ ). Red alder forest floor %N ( $2.4 \pm 0.07\%$ ) and litterfall %N ( $2.0 \pm 0.09\%$ ) were also significantly greater than Douglas-fir forest floor %N ( $1.4 \pm 0.07\%$ ) and litterfall %N ( $0.8 \pm 0.02\%$ ) across all sites ( $P < 0.001$  for both comparisons).

Soil %N was significantly greater ( $P < 0.05$ ) under red alder ( $0.38 \pm 0.02$ ) than Douglas-fir ( $0.28 \pm 0.03$ ), although soil C:N did not differ significantly ( $P = 0.08$ ) between red alder ( $17 \pm 1.8$ ) and Douglas-fir ( $23 \pm 2.3$ ). Enrichment factors ( $\epsilon_{\text{p-s}}$ ) indicated significantly greater ( $P = 0.001$ ) similarity in  $\delta^{15}\text{N}$  enrichment of foliage and soils in red alder sites ( $-3.3 \pm 0.19$ ) than in Douglas-fir sites ( $-4.5 \pm 0.18$ ).

Among individual trees, Douglas-fir foliar  $\delta^{15}\text{N}$  ranged from nearly  $-4.0\text{‰}$  to  $0.2\text{‰}$ , whereas red alder foliar  $\delta^{15}\text{N}$  was constrained tightly between  $-1.5\text{‰}$  to  $-0.5\text{‰}$  (Figure 2b). Ranges of  $\delta^{15}\text{N}$  in litterfall and forest floor were similar to those observed in the foliage of each species (Figure 3). The sample average  $\delta^{15}\text{N}$  for Douglas-fir litterfall and forest floor material ranged between  $-3.0\text{‰}$  and  $-1.0\text{‰}$ , whereas the range of sample average  $\delta^{15}\text{N}$  for red alder litterfall and



**Table 1. Linear regression results for riparian variables after accounting for within site correlations between trees**

	Estimate (SE)	Confidence limits for estimate	P value
Douglas-fir			
Foliar %N versus DFS	<b>-0.006 (0.003)</b>	<b>-0.011, 0.000</b>	<b>0.05</b>
Foliar $\delta^{15}\text{N}$ versus DFS	<b>-0.049 (0.018)</b>	<b>-0.086, -0.012</b>	<b>0.01</b>
Soil %N versus DFS	-0.001 (0.003)	-0.007, 0.005	0.784
Soil $\delta^{15}\text{N}$ versus DFS	<b>0.053 (0.017)</b>	<b>0.018, 0.089</b>	0.005
$\varepsilon_{\text{plant-soil}}$ versus DFS	<b>-0.103 (0.021)</b>	<b>-0.146, -0.059</b>	<b>&lt;0.001</b>
Foliar $\delta^{15}\text{N}$ versus soil $\delta^{15}\text{N}$	-0.125 (0.230)	-0.605, 0.356	0.594
Soil $\delta^{15}\text{N}$ versus soil %N	<b>-4.746 (1.166)</b>	<b>-7.186, -2.305</b>	<b>&lt;0.001</b>
Soil $\delta^{15}\text{N}$ versus soil C:N	<b>0.030 (0.008)</b>	<b>0.013, 0.047</b>	<b>0.002</b>
Soil %C versus DFS	0.124 (0.090)	-0.065, 0.312	0.186
Soil %C versus soil $\delta^{15}\text{N}$	1.617 (0.974)	-0.422, 3.656	0.114
Red alder			
Foliar %N versus DFS	-0.006 (0.006)	-0.018, 0.006	0.286
Foliar $\delta^{15}\text{N}$ versus DFS	0.001 (0.004)	-0.009, 0.010	0.898
Soil %N versus DFS	0.005 (0.003)	-0.002, 0.012	0.128
Soil $\delta^{15}\text{N}$ versus DFS	0.021 (0.011)	-0.003, 0.045	0.077
$\varepsilon_{\text{plant-soil}}$ versus DFS	-0.021 (0.012)	-0.046, 0.005	0.107
Foliar $\delta^{15}\text{N}$ versus soil $\delta^{15}\text{N}$	-0.001 (0.082)	-0.172, 0.171	0.994
Soil %C versus DFS	-0.071 (0.063)	-0.202, 0.060	0.273
Soil %C versus soil $\delta^{15}\text{N}$	1.083 (1.187)	-1.401, 3.567	0.373

DFS, distance from stream. The estimate is a weighted average of the regression coefficients of the response variable (e.g., foliar %N) on the independent variable (e.g., DFS) determined separately for each of the five sites.  $n = 5$  for all comparisons. Bold text indicates significant regressions at  $\alpha \leq 0.05$ .

forest floor was less, between  $-1.6\text{‰}$  and  $-1.0\text{‰}$ . All components of recognizable foliage (i.e., fresh foliage, litterfall, and forest floor) were depleted relative to mineral soil at all sites by an average of  $3.4\text{‰}$  for red alder and  $4.6\text{‰}$  for Douglas-fir (Figure 3).

## Discussion

The patterns of soil  $\delta^{15}\text{N}$  along riparian catenas at our study sites were not in agreement with our expectations on the basis of previous studies (Högberg 1997, Ben-David et al. 1998, Hedin et al. 1998, Helfield and Naiman 2002, Reimchen et al. 2003). Indeed, at our Douglas-fir sites, bulk soil  $\delta^{15}\text{N}$  patterns were opposite to what we anticipated; soils were more enriched in  $^{15}\text{N}$  at upslope positions instead of closer to the stream (Table 1; Figure 1a). At red alder sites, we found no relationship between soil  $\delta^{15}\text{N}$  and the position along a catena. It is, however, worthwhile to note that all foliage and litterfall samples in our data set were  $^{15}\text{N}$  depleted relative to mineral soils, in complete agreement with global patterns (Martinelli et al. 1999), yet in contrast to puzzling data showing foliage enriched samples relative to soils from the only other published study of plant and soil  $\delta^{15}\text{N}$  from Oregon Coast Range forests (Binkley et al. 1985). Below, we discuss how our results differ from the more widely established patterns in the literature and explore the possibility that red alder may be responsible for the discrepancy.

### Role of Anadromous Salmon

Inputs of N from spawning anadromous salmon are a unique feature of N biogeochemistry in riparian zones of the Pacific Northwest that can strongly influence N and  $\delta^{15}\text{N}$  patterns laterally away from streams (Reimchen et al. 2003).  $^{15}\text{N}$ -enriched inputs of marine-derived nitrogen from spawning and decaying salmon ( $>10.0\text{‰}$ ) have been shown to increase the  $\delta^{15}\text{N}$  of riparian plants and soils (Helfield

and Naiman 2002, Bilby et al. 2003, Koyama et al. 2005). Although anadromous salmon have been documented at most of our study sites our isotope data suggest a negligible influence on riparian N and  $\delta^{15}\text{N}$ . The  $\delta^{15}\text{N}$  of soil at Douglas-fir sites was more depleted nearer to the stream, contrary to the pattern expected if enriched  $^{15}\text{N}$  from salmon was a significant source of riparian N (Figure 1a) (Ben-David et al. 1998, Reimchen et al. 2003). In addition, two of our sites (one red alder and one Douglas-fir) were located above physical barriers to salmon migration, yet  $\delta^{15}\text{N}$  and %N of soil and foliage at these sites were indistinguishable from sites without barriers. We did observe that Douglas-fir foliar  $\delta^{15}\text{N}$  showed weak  $\delta^{15}\text{N}$  enrichment nearer to streams, although to a lesser degree than that observed in areas with significant salmon runs (Figure 2b) (Ben-David et al. 1998, Helfield and Naiman 2002, Reimchen et al. 2003).  $\delta^{15}\text{N}$  at red alder sites exhibited no catenal pattern, consistent with the idea that the importance of salmon-derived N decreases in the presence of N-fixing alder (Helfield and Naiman 2002). Despite speculation of an important role for salmon-derived N in watersheds of our study region (Reeves et al. 2002), we did not find strong evidence for such an effect in our study of riparian plant and soil N and  $\delta^{15}\text{N}$ .

### Denitrification and Nitrate Leaching

Denitrification is a common N cycling process that can be an especially important pathway of N loss in riparian zones with strong fractionating effects ( $\sim 30\text{‰}$ ) from  $\text{NO}_3^-$  source pools, resulting in N losses depleted in  $^{15}\text{N}$  (Hedin et al. 1998, Clement et al. 2003). If catenal variation in denitrification were the dominant process affecting  $\delta^{15}\text{N}$  at our sites, we would have expected greater enrichment of soil  $\delta^{15}\text{N}$  in wet low-lying areas nearer to streams (Sutherland et al. 1993) where reducing conditions are more likely to

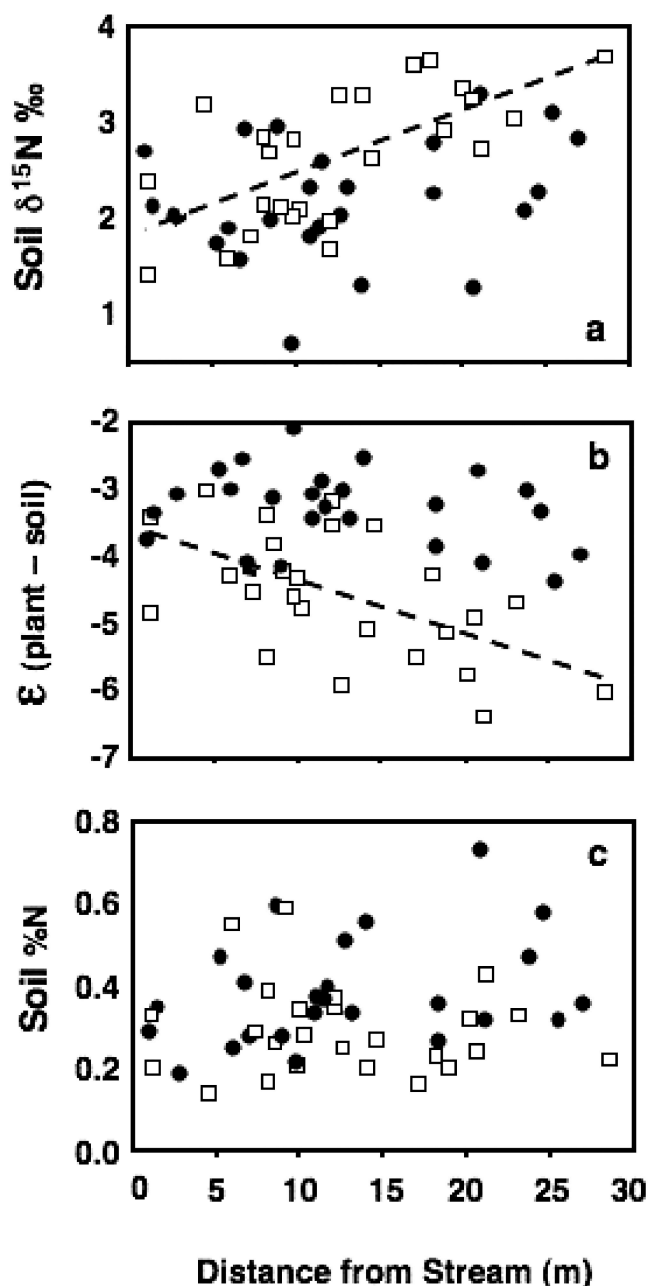


Figure 1. Patterns of (a) soil  $\delta^{15}\text{N}$ , (b) enrichment factors  $\epsilon_{\text{p-s}}$  of foliage minus soil  $\delta^{15}\text{N}$ , and (c) soil %N plotted against distance from the stream. Points indicate 0–10 cm depth mineral soil samples from Douglas-fir ( $\square$ ) and red alder ( $\bullet$ ) stands. Statistical significance of linear regressions is assessed as in Table 1 ( $P \leq 0.01$ ). For significant regressions, we have illustrated regression lines for Douglas-fir.

occur. However, in Douglas-fir sites, we observed the opposite pattern (Table 1; Figure 1a). We conclude that denitrification cannot explain the soil  $\delta^{15}\text{N}$  depletion nearer to streams in our Douglas-fir sites. Nitrification should also be favored by moist conditions nearer to streams and coupled with nitrate leaching would affect catenal  $\delta^{15}\text{N}$  signatures in a manner qualitatively similar to denitrification (Högberg 1997), but like denitrification this scenario is contrary to our observed soil  $\delta^{15}\text{N}$  patterns.

### Other Processes

It is not known whether riparian Douglas-fir rely on streamwater for N nutrition, but we can consider how this N

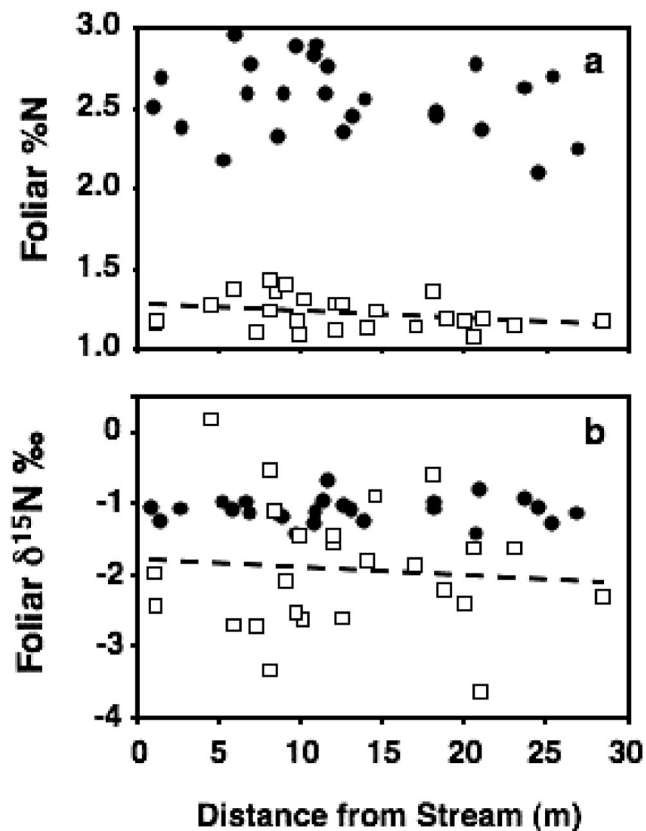


Figure 2. Patterns of (a) foliar %N and (b) foliar  $\delta^{15}\text{N}$  plotted against distance from the stream. Points indicate Douglas-fir ( $\square$ ) and red alder ( $\bullet$ ) foliage. Regression lines as in Figure 1.

flux might affect riparian catenal  $\delta^{15}\text{N}$  patterns. Nitrification of N fixed by red alder is the dominant source of streamwater nitrate across our study area (Compton et al. 2003). However, nitrification of available ammonium is incomplete in Coast Range soils ( $\approx 72\%$ ) (Hart et al. 1997), which should produce nitrate depleted by  $-10\text{‰}$  to  $-30\text{‰}$  (Högberg 1997). Yet, foliar  $\delta^{15}\text{N}$  of streamside Douglas-fir at our sites averaged  $-1.8\text{‰}$ , only marginally depleted relative to N fixed by red alder, suggesting that stream nitrate is likely only a negligible source of N for Douglas-fir. Moreover, Douglas-fir prefers ammonium over nitrate for its N nutrition (Bedell et al. 1999). Whereas Coast Range soils are rich in ammonium in proportion to soil total N (Perakis et al. 2006), streamwaters have low ammonium concentrations ( $<10 \mu\text{g}$  of N/L) relative to nitrate ( $0.074\text{--}2.043 \text{ mg}$  of N/L) (Compton et al. 2003), suggesting that streams may not provide a suitable root foraging environment for Douglas-fir nutrition.

Our results can also rule out catenal effects on soil mixing, disturbance, and age as potential explanations for our patterns. Greater mixing of mineral with organic soil might be expected near streams, driven by higher moisture for biota and stream erosional disturbance, both of which would decrease mineral soil  $\delta^{15}\text{N}$  in our samples by mixing in depleted  $\delta^{15}\text{N}$  from organic horizons. However, soil %C did not vary significantly with distance from stream (Table 1), which suggests no systematic variation in organic-mineral horizon mixing along our catenas. Potential effects of soil age (e.g., Amundson et al. 2003) are also unlikely to

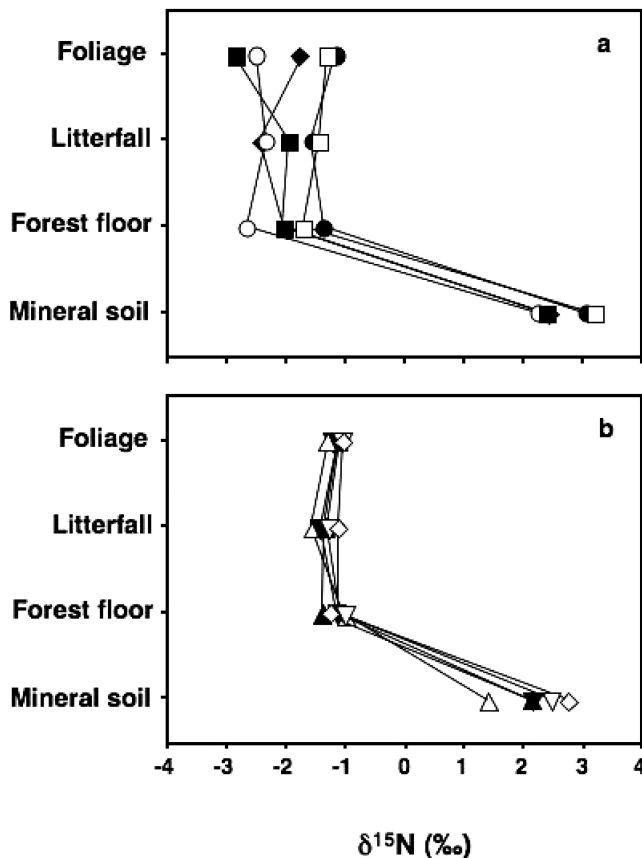


Figure 3.  $\delta^{15}\text{N}$  values of (a) Douglas-fir and (b) red alder foliage ( $n = 5$ ), litterfall ( $n = 2$ ), forest floor ( $n = 3$ ), and soils ( $n = 5$ ) for each site. Symbols indicate average values for individual Douglas-fir- and red alder-dominated sites.

explain the depletion in soil  $^{15}\text{N}$  near streams, owing to no systematic variation in soil  $\%C$  along catenas and because our riparian sites were not floodplain forests but rather were adjacent to constrained stream reaches that do not experience significant inundation by stream waters.

The age of our stands (40–100 years) places most of them at the time of midcentury logging. Logging has the potential to alter soil  $\delta^{15}\text{N}$  (Pardo et al. 2002). However, logging legacies on soil  $\delta^{15}\text{N}$  in our stands should be minimal. Coast Range watersheds do not exhibit a large pulse in nitrate loss after logging (Brown 1973), which is thought to be the cause of  $\delta^{15}\text{N}$  changes after logging at Hubbard Brook (Pardo et al. 2002). Moreover, the change in  $\delta^{15}\text{N}$  at Hubbard Brook was confined to organic horizons only, which returned to precut values within two decades. Our Douglas-fir sites are 40–100 years old, allowing for more than double the time for organic horizons to return to precut values. Additionally, mineral soils at Hubbard Brook did not change in response to logging (Pardo et al. 2002), which suggests our  $\delta^{15}\text{N}$  trend in catenal mineral soils is not a logging legacy.

### Role of Red Alder

Red alder is a pioneer tree species in the Pacific Northwest capable of sustaining exceptionally high N fixation rates (Binkley et al. 1994), with the ability to affect N cycling processes (Luken and Fonda 1983, Binkley et al.

1992, Compton et al. 2003). We found that foliage, litterfall, forest floor, and surface mineral soil  $\%N$  were significantly greater in red alder than in Douglas-fir stands, similar to differences observed in upland settings (Binkley et al. 1992). We also observed a narrower plant-soil isotopic enrichment ( $\epsilon_{p-s}$ ) under red alder than Douglas-fir, which may reflect inputs of recently fixed N to red alder soils (Myrold and Huss-Danell 2003). From foliage and litterfall isotope data, we surmise that red alder introduces fixed N at a very distinct and narrow  $\delta^{15}\text{N}$  signature ( $-1.1\text{‰} \pm 0.05$  [mean  $\pm$  SE]) (Figure 3). This narrow  $\delta^{15}\text{N}$  range of inputs, coupled with the high N fixation rates of red alder, provides a mechanism for red alder to exert strong leverage on soil  $\delta^{15}\text{N}$  that may explain the lack of observed catenal trends in soil  $\delta^{15}\text{N}$  at red alder sites. The consistently greater  $\delta^{15}\text{N}$  enrichment of soil relative to foliage in red alder sites also suggests that some portion of fixed N is subject to loss as isotopically depleted N, most likely via nitrate leaching and denitrification (Binkley et al. 1992).

Whereas we are unable to find evidence that salmon, streamside denitrification, logging, or other major N cycling mechanisms could explain the depletion of soil  $\delta^{15}\text{N}$  near streams in Douglas-fir sites, this trend may be a remnant of past red alder occupation along the stream. Soil  $\delta^{15}\text{N}$  near the stream approached a value of  $2\text{‰}$  at Douglas-fir sites (intercept in Figure 1a), similar to the average soil  $\delta^{15}\text{N}$  under red alder ( $2.2\text{‰}$  across all riparian positions at red alder sites). In upslope positions, the enriched  $\delta^{15}\text{N}$  of Douglas-fir soils may result from leaching losses of depleted  $\text{NO}_3^-$  that can occur in high N environments such as our sites (Martinelli et al. 1999), further contributing to the isotopic gradient we found. However, the lack of systematic catenal variation in soil  $\%N$  more likely precludes strong variations in nitrate leaching (Perakis et al. 2006). Finally,  $\epsilon_{p-s}$  values, which narrow at high soil N availability (Johannisson and Högberg 1994, Hobbie et al. 1999b, Schuur and Matson 2001), narrowed near the streams in our sites also suggesting that N was more available in this location along Douglas-fir catenas.

Soils contain  $>90\%$  of ecosystem N capital in coastal Pacific Northwest forests (Binkley et al. 1992), with soil N turnover occurring on the order of centuries, so we expect this pool to provide the strongest evidence of red alder legacies. The long-term persistence of red alder N in soil may be further enhanced by the high phenolic and N content of red alder litter, which facilitates N incorporation into stable soil organic matter pools (Bormann et al. 1994). However, the higher foliar N in Douglas-fir nearer to the stream (Figure 2a), with corresponding foliar  $\delta^{15}\text{N}$  ( $-1.8\text{‰}$ ) approaching that of red alder N ( $-1.1\text{‰}$ ), also raises the possibility that Douglas-fir accesses some N that was fixed by historical streamside red alder. This pattern of foliar  $\delta^{15}\text{N}$  does not occur in coniferous riparian forests that lack red alder and anadromous salmon (Reimchen et al. 2003, Koyama et al. 2005). Uptake of abundant streamwater nitrate may also influence near-stream Douglas-fir N and  $\delta^{15}\text{N}$  but has not been investigated and would not be favored by the preference of Douglas-fir for N as ammonium (Bedell et al. 1999). Such uptake (if it exists) would provide an additional mechanism for red alder influence on riparian

Douglas-fir N and  $\delta^{15}\text{N}$ , because most N in Coast Range streams originates from N fixation by red alder (Compton et al. 2003).

## Conclusions

Our foliar and soil N data suggest that N-fixing red alder can influence N biogeochemistry and isotopic signatures of Pacific Northwest riparian zones. The abundance of red alder in near-stream areas, its capacity for increasing soil N via high rates of symbiotic N fixation, and the tightly constrained  $\delta^{15}\text{N}$  of red alder N inputs all contribute a strong potential to influence soil N and  $\delta^{15}\text{N}$  signatures over time. These effects should be strongest immediately adjacent to streams, where red alder is most abundant in unmanaged riparian areas (Pabst and Spies 1999, Nierenberg and Hibbs 2000). Red alder is known to leave a legacy on foliar and soil N that persists for at least decades after site conversion to Douglas-fir (Brozek 1990) and is the most likely explanation for the uniquely high N status of many Oregon Coast Range soils (Perakis et al. 2006).

The exceptionally high rates of N input associated with red alder occurring at a tightly constrained  $\delta^{15}\text{N}$  signature could explain the high foliar N and depleted soil  $\delta^{15}\text{N}$  that we observed nearer to streams in riparian areas currently dominated by Douglas-fir. Just as fertilizer inputs of N can leave a legacy on soil  $\delta^{15}\text{N}$  (Johannisson and Högberg 1994, Högberg 1997, Koerner et al. 1999), we suggest that the historic occupancy of near-stream areas by N-fixing red alder may affect soil  $\delta^{15}\text{N}$  and plant N availability in riparian forests that are subsequently occupied by Douglas-fir, leaving a legacy effect on N biogeochemistry in these riparian sites.

## Literature Cited

- AMUNDSON, R.J., A.T. AUSTIN, E.A.G. SCHUUR, K. YOO, V. MATZEK, C. KENDALL, A. UEBERSAX, D. BRENNER, AND W.T. BAISDEN. 2003. Global patterns of the isotopic composition of soil and plant nitrogen. *Global Biogeochem. Cycles* 17:31-1-31-10.
- BEDELL, J.P., M. CHALOT, A. GARNIER, AND B. BOTTON. 1999. Effects of nitrogen source on growth and activity of nitrogen-assimilating enzymes in Douglas-fir seedlings. *Tree Physiol.* 19:205-210.
- BEN-DAVID, M., T.A. HANLEY, AND D.M. SCHELL. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: The role of flooding and predator activity. *Oikos* 83:47-55.
- BILBY, R.E., E.W. BEACH., B.R. FRANSEN, J.K. WALTER, AND P.A. BISSON. 2003. Transfer of nutrients from spawning salmon to riparian vegetation in western Washington. *Trans. Am. Fish. Soc.* 132:733-745.
- BINKLEY, D., K. CROMACK, JR., D.D. BAKER. 1994. Nitrogen fixation by red alder: biology, rates, and controls. P. 57-72 in *The Biology and Management of Red Alder*, Hibbs, D.E., D.S. Debell, and R.F. Tarrant (eds.). Oregon State University Press, Corvallis, OR.
- BINKLEY, D., P. SOLLINS, AND W.B. MCGILL. 1985. Natural abundance of nitrogen-15 as a tool for tracking alder-fixed nitrogen. *Soil Sci. Soc. Am. J.* 49:444-447.
- BINKLEY, D., P. SOLLINS, R. BELL, D. SACHS, AND D. MYROLD. 1992. Biogeochemistry of adjacent conifer and alder-conifer stands. *Ecology* 73:2022-2033.
- BORMANN, B. T., K. CROMACK, JR., AND W.O. RUSSELL III. 1994. Influences of red alder on soils and long-term ecosystem productivity. P. 47-56 in *The Biology and Management of Red Alder*, Hibbs, D.E., D.S. Debell, and R.F. Tarrant (eds.). Oregon State University Press, Corvallis, OR.
- BROWN, G.W., A.R. GAHLER., AND R.B. MARSTON. 1973. Nutrient losses after clear-cut logging and slash burning in the Oregon Coast Range. *Water Resour. Res.* 9:1450-1453.
- BROZEK, S. 1990. Effect of soil changes caused by red alder (*Alnus rubra*) on biomass and nutrient status of Douglas-fir (*Pseudotsuga menziesii*) seedlings. *Can. J. For. Res.* 20:1320-1325.
- CLEMENT, J., R. M. HOLMES, B. J. PETERSON, AND G. PINLAY. 2003. Isotopic investigation of nitrogen retention in a riparian ecosystem. *J. Appl. Ecol.* 40:1035-1048.
- COMPTON, J.E., M.R. CHURCH., S.T. LARNED, AND W.E. HOGSETT. 2003. Nitrogen export from forested watersheds in the Oregon Coast Range: The role of  $\text{N}_2$ -fixing red alder. *Ecosystems* 6:773-785.
- CORLISS, J.F. 1973. *Soil Survey of Alsea Area, Oregon*. US Soil Conservation Service, Washington, DC.
- EMMETT, B.A., O.J. KJØNAAS, P. GUNDERSEN, C. KOOPMANS, A. TIETEMA, AND D. SLEEP. 1998. Natural abundance of  $^{15}\text{N}$  in forests across a nitrogen deposition gradient. *For. Ecol. Manag.* 101:9-18.
- EVANS, R.D. 2001. Physiological mechanisms influencing plant nitrogen isotope composition. *Trends Plant Sci.* 6:121-126.
- FRANKLIN, J.F., AND C.T. DYRNES. 1988. *Natural Vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, OR.
- GARTEN, C.T., JR. 1993. Variation in foliage  $^{15}\text{N}$  abundance and the availability of soil nitrogen on Walker Branch Watershed. *Ecology* 74: 2098-2113.
- GARTEN, C.T., JR., AND H. VAN MIEGROET. 1994. Relationships between soil nitrogen dynamics and natural  $^{15}\text{N}$  abundance in plant foliage from Great Smoky Mountains National Park. *Can. J. For. Res.* 24:1636-1645.
- GREGORY, S.V., F.J. SWANSON., W.A. MCKEE, AND K.W. CUMMINS. 1991. An ecosystem perspective of riparian zones: Focus on links between land and water. *Bioscience* 8:540-551.
- HART, S.C., D. BINKLEY, AND D.A. PERRY. 1997. Influence of red alder on soil nitrogen transformations in two conifer forests of contrasting productivity. *Soil Biol. Biochem.* 29:1111-1123.
- HEDIN, L.O., J.C. VON FISCHER, N.E. OSTROM, B.P. KENNEDY, M.G. BROWN, AND G.P. ROBERTSON. 1998. Thermodynamic constraints on nitrogen transformations and other biogeochemical processes at soil-stream interfaces. *Ecology* 79:684-703.
- HELFIELD, J.M., AND R.J. NAIMAN. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. *Ecology* 82:2403-2409.
- HELFIELD, J.M., AND R.J. NAIMAN. 2002. Salmon and alder as nitrogen sources to riparian forests in a boreal Alaskan watershed. *Oecologia* 133:573-582.
- HOBBIE, E.A., AND J.V. COLPAERT. 2003. Nitrogen availability and colonization by mycorrhizal fungi correlate with nitrogen isotope patterns in plants. *New Phytol.* 157:115-126.
- HOBBIE, E.A., S.A. MACKO, AND H.H. SHUGART. 1999a. Insights into nitrogen and carbon dynamics of ectomycorrhizal and saprotrophic fungi from isotopic evidence. *Oecologia* 118:353-360.
- HOBBIE, E.A., S.A. MACKO, AND H.H. SHUGART. 1999b. Interpretation of nitrogen isotope signatures using the NIFTE model. *Oecologia* 120:405-415.
- HOBBIE, E.A., S.A. MACKO, AND M. WILLIAMS. 2000. Correlations between foliage  $\delta^{15}\text{N}$  and nitrogen concentrations may indicate plant-mycorrhizal interactions. *Oecologia* 122:273-283.



- HÖGBERG, P. 1997. Tansley Review No. 95:  $^{15}\text{N}$  natural abundance in soil-plant systems. *New Phytol.* 137:179–203.
- HURD, T.M., D.J. RAYNAL, AND C.R. SCHWINTZER. 2001. Symbiotic  $\text{N}_2$ -fixation of *Alnus incana* ssp. *rugosa* in shrub wetlands of the Adirondack Mountains, New York, USA. *Oecologia* 126:94–103.
- JOHANNISSON, C., AND P. HÖGBERG. 1994.  $^{15}\text{N}$  abundance of soils and plants along an experimentally induced forest nitrogen supply gradient. *Oecologia* 97:322–325.
- KOBA, K., M. HIROBE, L. KOYAMA, A. KOHZU, N. TOKUCHI, K.J. NADELHOFFER, E. WADA, AND H. TAKEDA. 2003. Natural  $^{15}\text{N}$  abundance of plants and soil N in a temperate coniferous forest. *Ecosystems* 6:457–469.
- KOERNER, W., E. DAMBRINE, J. L. DUPOUEY, AND M. BENOÎT. 1999.  $\delta^{15}\text{N}$  of forest soil and understorey vegetation reflect the former agricultural land use. *Oecologia* 121:421–425.
- KOOPMANS, C.J., D. VAN DAM, A. TIETEMA, AND J.M. VERSTRATEN. 1997. Natural  $^{15}\text{N}$  abundance in two nitrogen saturated forest ecosystems. *Oecologia* 111:470–480.
- KOYAMA, A., K. KAVANAGH, AND A. ROBINSON. 2005. Marine nitrogen in central Idaho riparian forests: Evidence from stable isotopes. *Can. J. Fish. Aquat. Sci.* 62:518–526.
- LUKEN, J.O., AND R.W. FONDA. 1983. Nitrogen accumulation in a chronosequence of red alder communities along the Hoh River, Olympic National Park, Washington. *Can. J. For. Res.* 13:1228–1237.
- MARTINELLI, L.A., M.C. PICCOLO, A.R. TOWNSEND, P.M. VITOUSEK, E. CUEVAS, W.H. McDOWELL, G.P. ROBERTSON, O.C. SANTOS, AND K. TRESEDER. 1999. Nitrogen stable isotopic composition of leaves and soil: Tropical versus temperate forests. *Biogeochemistry* 46:45–65.
- McKANE, R.B., L.C. JOHNSON, G.R. SHAVER, K.J. NADELHOFFER, E.B. RASTETTER, B. FRY, A.E. GIBLIN, K. KIELLAND, B.L. KWIATKOWSKI, J.A. LAUNDRE, AND G. MURRAY. 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature* 415:68–71.
- MYROLD, D.D., AND K. HUSS-DANEL. 2003. Alder and lupine enhance nitrogen cycling in a degraded forest soil in northern Sweden. *Plant Soil* 254:47–56.
- NADELHOFFER, K.J., AND B. FRY. 1988. Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. *Soil Sci. Soc. Am. J.* 52:1633–1640.
- NIERENBERG, T.R., AND D.E. HIBBS. 2000. A characterization of unmanaged riparian areas in the central Coast Range of western Oregon. *For. Ecol. Manag.* 129:195–206.
- OREGON DEPARTMENT OF FISH AND WILDLIFE. 2007. Natural Resources Information Management Program. Available online at [nrimp.dfw.state.or.us/nrimp/default.aspx](http://nrimp.dfw.state.or.us/nrimp/default.aspx); last accessed Jan. 9, 2008.
- PABST, R.J., AND T.A. SPIES. 1999. Structure and composition of unmanaged riparian forests in the coastal mountains of Oregon, USA. *Can. J. For. Res.* 29:1557–1573.
- PARDO, L.H., H.F. HEMOND, J.P. MONTOYA, T.J. FAHEY, AND T.G. SICCAMA. 2002. Response of the natural abundance of  $^{15}\text{N}$  in forest soils and foliage to high nitrate loss following clear-cutting. *Can. J. For. Res.* 32:1126–1136.
- PATCHING, W.R. 1987. *Soil survey of Lane County Area, Oregon*. US Soil Conservation Service, Washington, DC.
- PERAKIS, S.S., D.A. MAGUIRE, T.D. BULLEN, K. CROMACK, R.H. WARING, AND J.R. BOYLE. 2006. Coupled nitrogen and calcium cycles in forests of the Oregon Coast Range. *Ecosystems* 9:63–74.
- PETERSON, B.J., AND B. FRY. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* 18:293–320.
- REEVES, G.H., K.M. BURNETT, AND S.V. GREGORY. 2002. Fish and aquatic ecosystems of the Oregon Coast Range. P. 68–98 in *Forest and Stream Management in the Oregon Coast Range*, Hobbs, S.D., J. P. Hayes, R. L. Johnson, and G. H. Reeve (eds.). Oregon State University Press, Corvallis, OR.
- REIMCHEN, T.E., D.D. MATHEWSON, M.D. HOCKING, J. MORAN, AND D. HARRIS. 2003. Isotopic evidence for enrichment of salmon-derived nutrients in vegetation, soil and insects in riparian zones in Coastal British Columbia. *Am. Fish. Soc. Symp.* 34:59–69.
- RHOADES, C.C., AND D. BINKLEY. 1992. Spatial extent of impact of red alder on soil chemistry of adjacent conifer stands. *Can. J. For. Res.* 22:1434–1437.
- ROBINSON, D. 2001.  $\delta^{15}\text{N}$  as an integrator of the nitrogen cycle. *Trends Ecol. Evol.* 16:153–162.
- SAS INSTITUTE INC. 1999. SAS OnlineDoc, version 8 ed. SAS Institute, Inc., Cary, NC.
- SCHUUR, E.A.G., AND P.A. MATSON. 2001. Net primary productivity and nutrient cycling across a mesic to wet precipitation gradient in Hawaiian montane forest. *Oecologia* 128:431–442.
- SHEARER, G., AND D.H. KOHL. 1986.  $\text{N}_2$ -fixation in field settings: Estimations based on natural  $^{15}\text{N}$  abundance. *Aust. J. Plant Physiol.* 13:699–756.
- SUTHERLAND, R.A., C. VAN KESSEL, R. E. FARRELL, AND D.J. PENNOCK. 1993. Landscape-scale variations in plant and soil nitrogen-15 natural abundance. *Soil Sci. Soc. Am. J.* 57:169–178.
- TURNER, J., D.W. COLE, AND S.P. GESSEL. 1976. Mineral nutrient accumulation and cycling in a stand of red alder (*Alnus rubra*). *J. Ecol.* 64:965–974.